Zoological Journal of the Linnean Society (1992), *105:* 225–237. With 4 figures

Variation of apomorphic characters in stream-dwelling tadpoles of the bufonid genus *Ansonia* (Amphibia: Anura)

ROBERT F. INGER

Field Museum of Natural History, Chicago, Illinois, U.S.A.

Received May 1991, accepted for publication October 1991

Six larval forms of the bufonid genus *Ansonia* from Borneo share the following synapomorphies: cup-like, ventral oral disc; an expanded post-dental portion of the lower lip, which has a papillate margin; upper keratinized jaw sheath divided; body markedly flattened ventrally; eyes set relatively far back on the body. All of these tadpoles live on the bottom in strong currents, except for larval *Ansonia leptopus*, which lives in drifts of dead leaves that accumulate in eddies within streams. These larval forms differ among themselves in body shape, development of inframarginal papillae on the lower lip, size of the gap between the keratinized parts of the upper jaw sheath, width of the post-dental portion of the lower lip, relative lengths of upper and lower rows of labial teeth, and arrangement of the gut coils. One form has an abdominal sucker. Changes in these characters are not correlated; the derived condition in one character is not always associated with the derived state in another. Consequently, these tadpoles cannot be arranged in a simple morphocline from least to most derived, again with the exception of *A. leptopus*, which is the least modified in all respects. Although tadpoles of *Ansonia* resemble those of the neotropical bufonid genus *Atelopus* in general specialization for benthic life in flowing water, they differ from that group in body form and details of the oral disc.

KEY WORDS:—Benthic – tadpoles – streamlining, variation, specialization.

CONTENTS

INTRODUCTION

Despite the constraints of the general body plan of tadpoles—a very short trunk, a very long gut, gills and developing forelimbs under an operculum—these animals have managed a remarkable adaptive radiation. The long-term interest in this radiation (e.g. Noble, 1931; Orton, 1953; Mertens, 1960) and its concomitant phenomenon, convergence, has culminated in a comprehensive review of the guilds of anuran larvae by Altig & Johnston (1989), who outline in detail the external morphological features associated with the

0024–4082/92/060225+13 $03.00/0

various ecomorphotypes. Study of variation within one of these ecomorphotypes within a lineage has been relatively infrequent, one of the early examples being Noble's (1931) work on Jamaican hylid tadpoles living in small water reservoirs of epiphytes. A more detailed recent example is the study by Wassersug & Duellman (1984) of the oral structures of the larvae of hylid frogs having brood pouches. In this paper I will consider the interspecific variation of the benthic, stream-dwelling tadpoles of a genus of Bufonidae.

Larvae of south-east Asian genera of Bufonidae are of three general types. The first, characteristic of *Bufo*, *Pedostibes* and *Leptophryne*, and resembling generalized larval *Bufo* elsewhere, has a slightly flattened, globular, black body, weakly serrated jaw sheaths, upper rows of labial teeth equal in length to lower ones, papillae restricted to the sides of the oral disc (except in *Leptophryne*), and spiral gut coils (Inger, 1985). A second type, exemplified by larvae of *Pelophryne*, has an ovoid body, labial teeth reduced to a single short row, feebly crenulate, rather than papillate lips, and the gut with only two or three thick coils; apparently they subsist solely on the yolk supply of the large egg (Inger, 1960).

The third type, associated with *Ansonia*, has a cup-like oral disc with expanded lips, smooth weak jaw sheaths with the upper one divided into two keratinized portions, a complete row of marginal papillae across the expanded lower lip, and a body that is markedly flattened ventrally (Inger, 1985). In the terminology of Altig & Johnston (1989), these are typical lotic-suctorial, type 1 tadpoles. A distinct larval morphotype is part of the basis for recognition of this genus (Inger, 1954), as is true for some bufonid genera in other continents, e.g. *Stephopaedes* (Channing, 1978).

Six Bornean larval forms of *Ansonia* display an array of modifications showing that the possibilities for diversification have not been restricted by the obligate benthic morphotype. These modifications involve papillation of the lips, structure of the jaw sheaths, relative lengths of rows of labial teeth, coiling of the gut, and shape of the body. The variations in each character can be arranged into grades of increasing departure from the typical bufonid tadpole, although variations are not correlated across characters. The purpose of this paper to describe this variation and to consider its relationship to the benthic habits of these larvae.

MATERIALS AND METHODS

All tadpoles, except those of *A. leptopus*, were collected by means of electroshocking in clear, rocky streams. All were anaesthetized with chlorobutanol within 2 hours, preserved in buffered formalin, and stored in that preservative in the collections of Field Museum of Natural History (FMNH). A sample of *Ansonia muelleri* tadpoles from Mindanao (FMNH 50902-05), collected in 1946–47 and preserved in 70% ethanol was also examined. They are badly shrivelled and provide only limited information on certain characters. In addition to the *Ansonia* tadpoles listed in Appendix, larvae of *Bufo veraguensis*, *Atelophryniscus chrysophorus*, *Atelopus pachydermus* and *Atelopus* sp. were examined in the collection of United States National Museum of Natural History (USNM).

Larvae were staged according to the system of Gosner (1960) and measured at 12 × magnification using an ocular grid. Scanning electron microscopy was used to study the buccopharynx of four species. Because the subject of this paper is

the pattern of specializations, the descriptions of each form will be confined to those structures or characters involved in that pattern or those that serve to distinguish each form from the others. Statistical analyses were carried out using SYSTAT. Tests applied to data are noted at appropriate points in the text. Abbreviations used: HB = head-body, HBL = head-body length, HBW = head-body width. Measurements follow Inger (1985). Terminology of buccopharyngeal structures is that of Wassersug (1976), and numeration of labial tooth rows follows Altig's (1970) system.

SPECIES IDENTIFICATION

Assigning these larval forms to the genus *Ansonia* is relatively simple. All larvae in stages > 39 have slender digits and limbs and weak subarticular tubercles, features distinguishing *Ansonia* from *Bufo* and *Pedostibes*. The six larval forms share a number of characters that, within the Bufonidae, are almost certainly derived: HB distinctly flattened below; oral disc ventral; both lips with wide areas peripheral to the tooth rows; lower lip with a continuous border of papillae; upper jaw sheath divided into two separated, keratinized pieces. These synapomorphies distinguish these larvae from all other bufonid larvae occurring in south-east Asia and adjacent islands. In addition, the four forms whose buccopharynges have been examined (*leptopus*, *longidigita*, *spinulifer*, 'sucker') share the following characters: tongue anlage distinct, buccal floor with smooth interior, buccal roof lacking papillae or pustules, prenarial area with a single, large median papilla and narial valves drawn out medially into flaps pressed flat against the roof and extending obliquely forward into the prenarial area. None of these buccopharyngeal characters occurs in other Bornean bufonids which have been examined: *Bufo asper*, *B. divergens* and *Pedostibes hosei* (Inger, 1985).

Post-metamorphic ontogenetic changes in colouration, webbing and features of the dorsal skin complicate assignment of larvae to species of adults. I have assigned larvae to *A. spinulifer* and *A. longidigita* using extensive pre- and metamorphic series, with the most advanced individuals matching adults, and on the co-occurrence of larvae and adults at two or more localities. Larvae assigned to *A. leptopus* were abundant along four streams (two localities) where adults of this species were also abundant.

The other three larval types cannot be assigned to species at this time. However, the tentative nature of species assignments does not interfere with analysis of morphological trends; it merely causes some awkwardness of language. Certainly there is little question concerning specific distinctiveness of these larval forms, as each can be defined by a unique combination of three or four characters.

Ansonia leptopus (Guenther)

HB oval, snout rounded in dorsal view, body widest midway between eyes and end of body; eyes dorsolateral; eye-snout distance 0.21–0.28 of HBL; nostril-snout distance 0.14–0.21 of HBL. Oral disc narrower than body; distance from lower jaw sheath to P3 about twice distance from P3 to margin of lip; upper lip with marginal papillae in lateral fourth; lower lip with a short row of low, thick inframarginal papillae in lateral third; upper rows of labial teeth ending in line with lower rows; gap between halves of upper jaw sheath 0.2–0.8 length of one

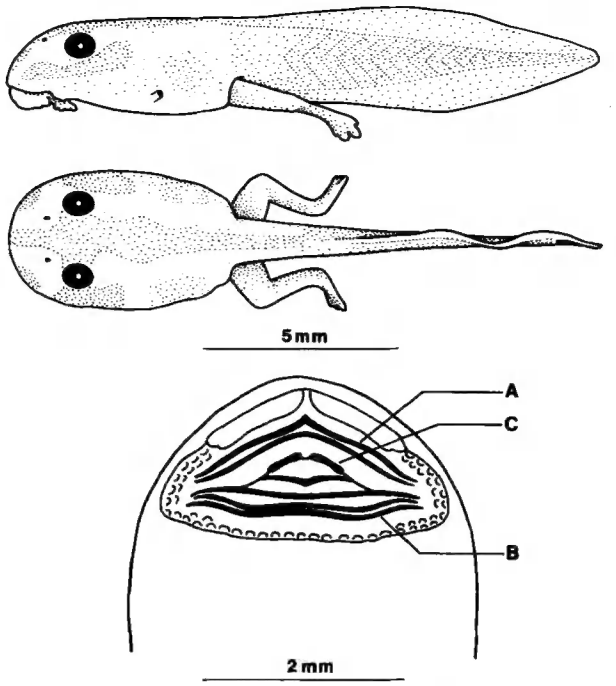

Figure 1. *Ansonia leptopus*. Lateral (top) and dorsal (middle) views of tadpole and oral disc (bottom). A, Anterior and B, posterior rows of denticles. C, Half of keratinized anterior beak. Margin of anterior lip folded over.

half; lower jaw sheath not divided. No abdominal sucker; gut mass spiral. Tail height 0.26–0.35 of tail length; tapering to rounded tip in distal half; origin of dorsal fin at end of body. In stages < 39, HB white with black median stripe from tip of snout to end of tail, passing between eyes and along dorsal margin of caudal muscle; a wide interorbital black band; a dark area behind and below eye, extending forward as narrow stripe parallel to ventral margin of snout.

Tongue anlage with two pairs of lingual papillae in anterior third; buccal floor arena with 4–5 large, conical papillae on each side.

HBL 3.3–5.8 mm, stages 25–39 ($N = 22$).

Ansonia longidigita Inger

HB almost teardrop-shaped, snout broadly rounded in dorsal view, body widest in plane through front margin of eyes; a distinct ventrolateral constriction at postorbital plane; eyes dorsolateral; eye-snout distance 0.29–0.38 of HBL; nostril-snout distance 0.22–0.29 of HBL. Oral disc narrower than maximum body width; distance from lower jaw sheath to P3 about half distance from P3 to margin of lip; margin of upper lip smooth; lower lip with two or three irregular rows of low, thick inframarginal papillae; upper rows of labial teeth ending far lateral to and behind lower rows; gap between halves of upper jaw sheath 2.8–3.3 times length of one half; lower jaw sheath not divided. No abdominal sucker; gut mass spiral. Tail height 0.19–0.21 of tail length, tail tapering to pointed tip in distal two-fifths; origin of dorsal fin near midpoint of tail. HB uniformly black dorsally and laterally.

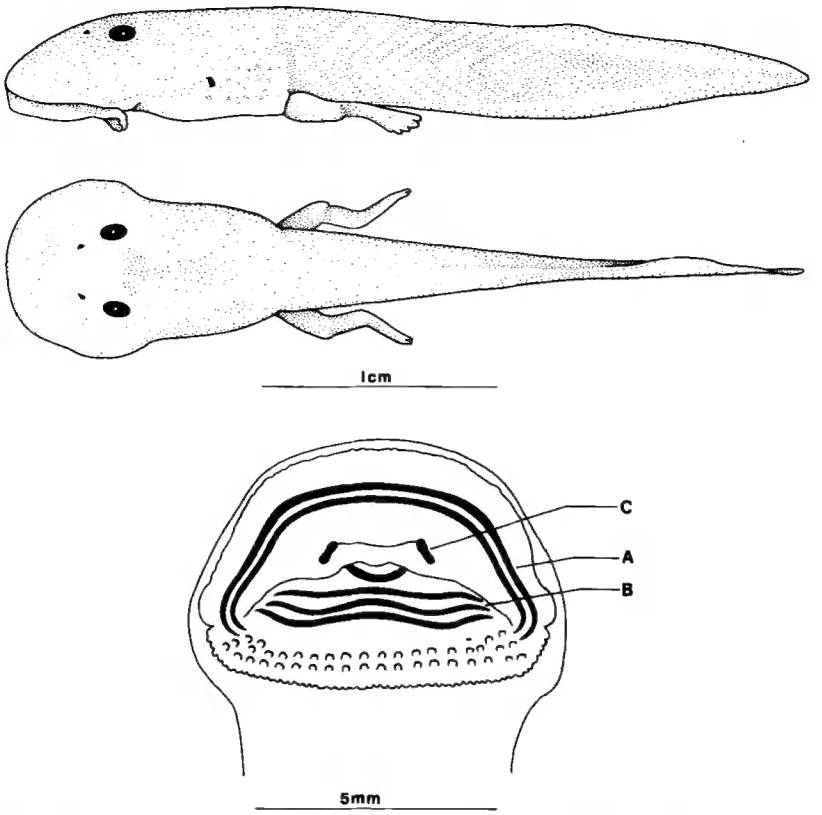

Figure 2. *Ansonia longidigita*. Lateral (top) and dorsal (middle) views of tadpole and oral disc (bottom). A, Anterior and B, posterior rows of denticles. C, Half of keratinized anterior beak.

Tongue anlage with a pair of thick, apically bifid, papillae in anterior third; buccal floor arena with 6–8 conical papillae on each side.

HBL 8.8–11.9 mm, stages 32–41 ($N = 63$).

Ansonia spinulifer (Mocquard)

HB ovoid, snout broadly rounded in dorsal view, body widest in plane just before eyes; eyes dorsal; eye-snout distance 0.28–0.37 of HBL; nostril-snout distance 0.19–0.26 of HBL. Oral disc as wide as or slightly narrower than HBW; distance from lower jaw sheath to P3 approximately equal to distance from P3 to margin of lip; upper lip with marginal papillae at lateral fifth; lower lip with two rows of low, thick, round inframarginal papillae; upper rows of labial teeth ending far lateral to but not behind ends of lower rows; gap between halves of upper jaw sheath 1.5–2.2 times length of one half; lower jaw sheath not divided. No abdominal sucker; gut mass spiral. Tail height 0.17–0.22 of tail length; tail tapering to a narrow, rounded tip in last third; origin of dorsal fin beginning posterior to proximal fourth of tail. HB uniformly black dorsally and laterally.

Tongue anlage with a pair of long, thick papillae in posterior third; buccal floor arena with 6–8 thick papillae laterally and a clump of 6–10 pustules posterolaterally.

HBL 4.8–8.3 mm, stages 26–41 ($N = 22$).

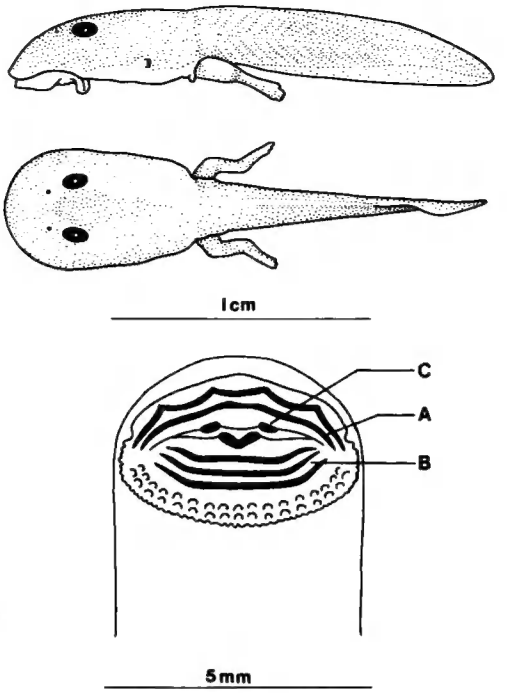

Figure 3. *Ansonia spinulifer*. Lateral (top) and dorsal (middle) views of tadpole and oral disc (bottom). A, Anterior and B, posterior rows of denticles. C, Half of keratinized anterior beak.

Ansonia 'cruciform'

HB teardrop-shaped, snout broadly rounded in dorsal view, body widest in plane just before or through eyes; eyes dorsolateral; eye-snout distance 0.29–0.35 of HBL; nostril-snout distance 0.20–0.25 of HBL. Oral disc wider than body; distance from lower jaw sheath to P3 two-thirds of distance from P3 to margin of lip; upper lip with marginal papillae in lateral fifth; lower lip without inframarginal papillae; upper rows of labial teeth ending lateral to upper rows, but not curling behind them; gap between halves of upper jaw sheath 1.2–2.2 times length of one half; lower jaw sheath not divided. No abdominal sucker; gut mass in transverse coils. Tail height 0.24–0.29 of tail length; tail tapering in distal third to rounded tip; origin of dorsal fin after proximal eighth of tail. Body with cruciform pattern; median longitudinal light band from tip of snout intersecting light transverse preorbital band; light transverse postorbital band beginning low on side but not reaching vertebral line.

HBL 4.8–6.1 mm, stages 32–37 ($N = 6$).

Ansonia 'sucker'

HB teardrop-shaped, snout very broadly rounded in dorsal view, body widest in plane through anterior border of eyes; a distinct ventrolateral notch on snout in plane between nares and eyes; eyes dorsal; eye-snout distance 0.26–0.36 of HBL; nostril-snout distance 0.17–0.25 of HBL. Oral disc slightly narrower than widest part of body; distance from lower jaw sheath to P3 equal to distance from P3 to margin of lip; upper lip with small marginal papillae in lateral fifth and minute ones across remainder of margin; lower lip without inframarginal

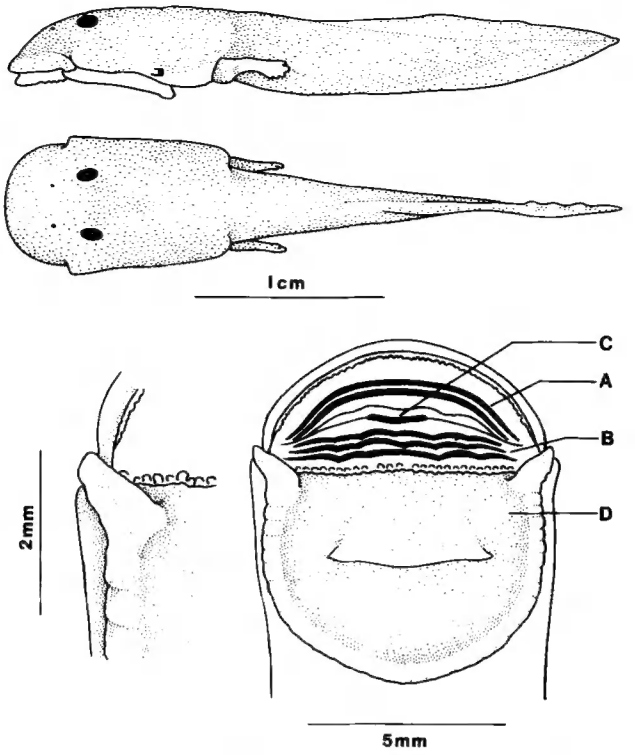

Figure 4. *Ansonia* larva with abdominal sucker (D). Lateral (top) and dorsal (middle) views of tadpole, oral disc (bottom right), and detail of ventrolateral notch (bottom left). A, Anterior and B, posterior rows of denticles. C, Keratinized posterior beak; no anterior keratinized beak. D, Sucker.

papillae; upper rows of labial teeth ending in line with those of lower lip; no keratinized upper jaw sheath; lower jaw sheath not divided.

A sharply defined abdominal sucker with free lateral and posterior borders immediately behind oral disc; sucker slightly narrower than body; an oblique pocket present on each side medial from lateral margin, opening mesad; a transverse pocket facing forward between posterior ends of lateral ones; distance from tip of snout to posterior edge of sucker 0.70–0.78 of HBL.

Gut mass constricted in rostrocaudal axis and shifted caudally; coils arranged transversely with lateral margins twisted caudally and dorsally.

Tail height 0.17–0.25 of tail length; tail tapering in distal third to sharp point; origin of dorsal fin at end of proximal third of tail. HB black dorsally and laterally.

Tongue anlage with a pair of minute papillae; buccal floor arena with 7 papillae laterally.

HBL 10.7–13.0 mm, stages 34–38 ($N = 7$).

Ansonia 'beaks divided'

HB oval, snout broadly rounded in dorsal view, body widest in plane before eyes; eyes dorsolateral; eye-snout distance 0.28–0.34 of HBL; nostril-snout distance 0.19–0.26 of HBL. Oral disc as wide as body; distance from lower jaw sheath to P3 equal to distance from P3 to margin of lip; upper lip with marginal

papillae restricted to corners; lower lip with one continuous row of low, thick inframarginal papillae; upper rows of labial teeth longer than upper ones, ending laterad from lower rows but not curling around them; both jaw sheaths usually divided, lower one merely thinned medially in one larva; gap between halves of upper jaw sheath 2.7–4.3 times length of one half; gap between halves of lower jaw sheath 0.3–0.6 times length of one half. No abdominal sucker; gut mass spiral. Tail height 0.17–0.20 of tail length; tail tapering in distal third to narrow rounded tip; origin of dorsal fin at end of proximal third of tail.

HB black dorsally and laterally, with a light round area behind eye and another ventrolaterally on snout before level of eyes. HBL 6.4–7.7 mm, stages 39–41 ($N = 4$).

DISCUSSION

These six larval forms of *Ansonia* differ from one another in various ways, including degree of departure from typical bufonid form. Body shape varies from ovoid, with the widest part of the body between the eyes and the end of the body as in most bufonid larvae (*leptopus*), to teardrop-shaped with the widest part of the body in a plane through the front of the orbits. This difference in shape does not affect maximum relative body width, although there are significant interspecific differences in that character (Table 1). *Ansonia leptopus*, the least modified of these larval forms, lives in leaf drifts (Inger, 1985) and is the only one that does not live in torrents.

The position of the eyes relative to the snout also varies significantly among species (orbit-snout, Table 1), with *leptopus* having the eyes much closer to the tip of the snout than the other forms. Even in *leptopus*, however, the eyes are farther to the rear than in other Bornean bufonid larvae [orbit-snout/HBL < 0.23 in larval *Bufo divergens* ($N = 5$), *B. asper* ($N = 6$), and *Pedostibes hosei* ($N = 5$)]. The relationship of eye position to life in strong currents is not clear. However, among ranoid tadpoles, the eye is set farther back in torrent-dwelling *Amolops* tadpoles (in six species, orbit-snout/HBL 0.27–0.39, $N = 25$) than in larval *Rana* living in weak currents (in six species, orbit-snout/HBL 0.13–0.24, $N = 27$).

An expanded oral disc is one of the striking divergences of larval *Ansonia* from the typical bufonid morphotype. Differences among species of *Ansonia* are significant (Table 1), yet all have much wider oral discs (oral disc width/HBL > 0.46) than do other bufonid larvae from the same areas (*Bufo asper* 0.29–0.34, $N = 5$; *B. divergens* 0.28–0.36, $N = 11$; *Pedostibes hosei* 0.28–0.43, $N = 9$). The degree of expansion of the lower lip also varies among species. The relative widths of the dental and post-dental portions of the lip, measured in the rostrocaudal axis, vary from a 2 : 1 ratio (in *leptopus*) to 1 : 2 (in *longidigita*), with intermediate ratios of 1 : 1 in *spinulifer*, 'sucker' and 'beaks divided' and 1 : 1.5 in 'cruciform' and *muelleri*. All have a complete fringe of marginal papillae across the lower lip, but the number of inframarginal rows varies from none in 'cruciform' and 'sucker' to two or three rows in *longidigita*. In most larval *Ansonia* the upper lip is smooth except near the corner, but in 'sucker' the entire margin is crenulated, and in the Philippine *muelleri* the margin is papillate except in the median third.

The upper rows of labial teeth are much longer than the lower ones in half of these larval forms. In *longidigita*, the upper rows extend beyond and curl back

TABLE 1. Differences among larval *Ansonia* in body proportions. All character values given as proportions of head-body length

Species	Head-body width			Orbit-snout			Oral disk width			Gap in beak	
	N	Range	Median	*N*	Range	Median	*N*	Range	Median	*N*	Range	Median
'Beaks divide'	3	0.62–0.69	0.644	4	0.28–0.34	0.291	4	0.55–0.71	0.622	4	0.14–0.16	0.152
'Cruciform'	8	0.62–0.68	0.648	8	0.27–0.34	0.310	8	0.67–0.73	0.694	8	0.08–0.12	0.100
A. leptopus	20	0.62–0.73	0.667	22	0.21–0.28	0.250	15	0.47–0.59	0.529	17	0.01–0.04	0.029
A. longidigita	23	0.62–0.73	0.667	18	0.29–0.43	0.376	25	0.56–0.70	0.631	22	0.12–0.16	0.140
A. spinulifer	17	0.59–0.69	0.649	10	0.28–0.37	0.320	16	0.58–0.71	0.623	19	0.09–0.12	0.102
Sucker	10	0.60–0.66	0.634	10	0.26–0.36	0.300	5	0.55–0.60	0.598	—*		
H†		15.72			54.90			44.08			66.21	
P		0.008			<0.001			<0.001			<0.001	

*Species lacks upper keratinized beak.
†H of Kruskal-Wallis test.

TABLE 2. Relation of size to stage of development in tadpoles of *Ansonia*. Size is given in terms of HBL (mm)

	HBL at stages			
Species	26–30	31–34	35–37	38–41
A. leptopus	4.1–4.4	4.8–5.4	5.0–5.8	5.6–5.8
A. longidigita	6.8–10.3	7.9–11.1	10.3–11.7	10.3–11.5
A. spinulifer	4.8–5.2	5.2–6.7	6.8–7.9	7.8–8.3
'Cruciform'	4.8–5.1	4.8–6.1	5.2–5.5	
'Beaks divided'				6.4–7.7
'Sucker'	7.6–9.3		11.4–12.5	11.8–12.8

behind the level of the lower rows (Fig. 2). In 'beaks divided' and in *spinulifer* (Fig. 3), the upper rows end lateral to but do not curl around the ends of the lower rows. In *leptopus* (Fig. 1), 'cruciform', 'sucker' (Fig. 4) and *muelleri*, the upper rows end in about the same rostrocaudal axis as the lower rows.

The last feature of the oral disc of larval *Ansonia* that is clearly apomorphic is the division of the upper jaw sheath into two keratinized pieces. The gap between the two pieces is narrowest in *leptopus* and is at least four times wider in the other forms, with significant variation among them (Table 2). The extreme state occurs in 'sucker', which has no keratinized upper jaw sheath. In 'beaks divided' and *muelleri*, the lower jaw sheath is also divided.

The usual, and presumably, primitive arrangement of the gut in bufonid (and most other) tadpoles is as a spiral, and that is also the arrangement in most *Ansonia* tadpoles. However, in three forms, *muelleri*, 'cruciform' and 'sucker', the gut coils have a distinctly transverse arrangement, and in the last species the ends of each coil are curved caudally and dorsally. A functional explanation for the transverse coils of 'cruciform' and *muelleri* is not obvious. Other species, for example, larval *longidigita*, have equally streamlined, depressed bodies and the same habit of clinging to rocks in torrents, yet retain the ancestral circular coiling of the gut. The intestinal coils of 'sucker' resemble those of the gastromyzophorous tadpoles of the ranid *Amolops*.

Ansonia 'sucker' is alone among these larval *Ansonia* in having an abdominal sucker and therefore falls in a different guild within the system of Altig & Johnston (1989). In addition to its sharply defined, raised borders, this structure has a pair of retractor muscles corresponding to the diaphragmatobranchialis medialis and the diaphragmatopraecordialis found in larval *Amolops* (Noble, 1929). The presence of these muscles running through the region usually occupied by the gut coil may account for the peculiar arrangement of the gut in *Ansonia* 'sucker' and *Amolops*. The external form of the sucker is much like that of the suckers of larval *Atelopus*, except that there are no folds or pockets within the sucker in *Atelopus*. There is no indication of a precursor to the abdominal sucker in any of the other *Ansonia* tadpoles, not even a post-oral depression, such as occurs in larval *Bufo veraguensis* (Cadle & Altig, 1991) or *Rana sauteri* (Kuramoto, Wang & Yu, 1984).

Two conclusions can be drawn from these observations: First, changes in the structures involved in the departure of larval *Ansonia* from the presumed primitive larval bufonid have not been closely linked. The widest oral disk is not associated with the development of an abdominal sucker. The derived type of

gut coiling is not associated with a teardrop-shaped body or with the greatest disparity between lengths of upper and lower rows of labial teeth. The second conclusion is that these larval *Ansonia* cannot be arranged into a simple morphocline from least to most derived, although in shape of body, position of the eyes and most features of the oral disc, larval *leptopus* is least divergent from the typical bufonid morphology. *Ansonia* 'sucker', in some respects the most modified (e.g. sucker, loss of upper jaw sheath), occupies an intermediate position in terms of the expansion of the lower lip and relative lengths of upper and lower rows of labial teeth. *Ansonia* 'cruciform' has transverse coiling of the gut, but its body shape is not as modified as that of *longidigita* which, however, has the typical bufonid spiral intestinal coiling.

Do any of these interspecific differences suggest differences in specialization for benthic life in flowing waters? In particular, do they suggest differences in drag-reducing mechanisms? [Larval *leptopus* are omitted from this part of the discussion because, living in leaf drifts, they avoid the force of a current.] As all of these tadpoles live attached to rocks at approximately the same depth, in torrents having currents about 1.0–1.5 ms^{-1}, we can ignore differences in kinematic viscosity of the medium. This simplifying assumption allows us to calculate Reynolds numbers, the critical measure of how animals of varying shapes and sizes interact with moving fluids, as the product of cross-sectional area of the tadpole normal to the direction of flow and current velocity. Interspecific variation in Reynolds numbers of these larval forms has a range of $7.7–24.3 \times 10^3$ at the lower current velocity and $1.2–3.6 \times 10^4$ at the higher. In either case the range, less than an order of magnitude, is probably too small to be biologically significant (Vogel, 1981). With Reynolds numbers in these ranges, streamlining can significantly reduce drag (see examples in Vogel, 1981), and can be measured in two ways: total length divided by maximum width, and distance to plane of maximum width divided by total length, both approximating the degree of tapering. Differences among larval forms of *Ansonia* in both these ratios are statistically significant (Kruskal-Wallis ANOVA: $H > 19.4$, d.f. $= 4$, $P < 0.01$), and in both, *Ansonia* 'beaks divided' has the most streamlined form and *Ansonia* 'cruciform' the least.

However, body shape may not be the sole or overwhelmingly important factor affecting the relation of these tadpoles to water flow. We do not know the functional significance of relative widths of the dental and post-dental portions of the lower lip, or of the papillae on the lip. Variations in these (and perhaps other characters) may be important to maintenance of position in strong currents. Furthermore, there are no measurements of current precisely where individual tadpoles were attached, merely 'average' measurements in torrents where tadpoles were collected.

The Neotropical bufonid *Atelopus* has larvae similar in some respects to those of *Ansonia*. Excluding *Ansonia leptopus* (a leaf drift dweller), most lots (86–97%) of larval *Ansonia* were captured in riffles and torrents, precisely the types of microhabitats utilized by larval *Atelopus* (Duellman & Lynch, 1969). Morphologically the two groups of larvae share some features: both have expanded, ventral oral discs and both have bodies flattened ventrally; abdominal suckers appear in one larval form of *Ansonia* but in all larvae of *Atelopus*. Differences between the two groups, however, are striking. Larval *Atelopus* have oval bodies with the widest part well behind the eyes (see

illustrations in Duellman & Lynch, 1969); in all larval *Ansonia* except *leptopus* maximum body width is in a plane through or in front of the orbits. Although tadpoles of *Atelopus* are flattened ventrally, they have rather deep bodies, and none are as depressed as most tadpoles of *Ansonia* (Figs 1–4). The lower lip of larval *Atelopus*, like that of *Bufo*, is coterminous with the outer row of labial teeth except near the corners. In contrast, all tadpoles of *Ansonia* have a papillate extra-dental expansion of the lower lip, which may be important in the adherence of the oral disc to the substrate (Altig & Johnston, 1989).

Several differences between larval *Ansonia* and *Atelopus* in body shape suggest functional/ecological differences. Although *Atelopus* has slightly higher Reynolds numbers ($3.6–4.2 \times 10^4$), the difference is not significant (i.e. still much less than an order of magnitude). However, larval *Atelopus* have less streamlined forms; the ratios of total length to maximum width are 3.2–3.7 in *Atelopus* and 3.8–5.0 in *Ansonia* of comparable length, and the plane of maximum width is much farther from the snout in *Atelopus*. The bodies of *Atelopus* tadpoles are also deeper than those of *Ansonia*, exposing them more to pressure drag as current becomes stronger away from the bottom. Possibly, the abdominal suckers present in larval *Atelopus* compensate for the presumed increased drag resulting from this body shape. Paradoxically, the larval *Ansonia* with a body shape most similar to that of larval *Atelopus* is *leptopus*, the species most different ecologically from larval *Atelopus*.

Finally, although the biological significance is unclear, the pattern of variation seen in these tadpoles of *Ansonia* also occurs in at least two other torrent-adapted groups. In rocky, high-gradient streams in Borneo, *Ansonia* tadpoles may be observed clinging to the same rock as tadpoles of *Amolops* and fishes of the genus *Gastromyzon*. In both of the last two, as in *Ansonia*, there is interspecific variation in structures that are involved in the specialized habits: degree of expansion of the oral disc and form of the keratinized jaw sheaths in larval *Amolops* (Inger, 1985), and form of the mouth and relative lengths of the ventral sucker in *Gastromyzon* (Roberts, 1982; Chin & Inger, 1989).

ACKNOWLEDGEMENTS

Many persons helped with the collection of specimens and data in the field. In particular I want to acknowledge the help of F. L. Inger, R. B. Stuebing, H. K. Voris and P. Yambun. I am also grateful to Ghazally Ismail (Universiti Kebangsaan Malaysia, Sabah Kampus), Lamri Alisaputra (Sabah Parks), and Sim Boon Liang (Sabah Forest Industries) for the use of facilities and logistical support, and to R. Altig, S. B. Emerson, R. W. McDiarmid and R. J. Wassersug for their helpful comments and suggestions. Figures 1–4 were prepared by Z. Jastrzebski. Partial support for field work came from grants from National Science Foundation, National Geographic Society, Marshall Field III Fund of Field Museum of Natural History, and the Allen-Heath Memorial Foundation.

REFERENCES

ALTIG, R., 1970. A key to the tadpoles of the continental United States and Canada. *Herpetologica, 26:* 180–207.

ALTIG, R. & JOHNSTON, G. F., 1989. Guilds of anuran larvae: relationships among developmental modes, morphologies, and habitats. *Herpetological Monographs, 3:* 81–109.

CADLE, J. E. & ALTIG, R., 1991. Two lotic tadpoles from the Andes of southern Peru: *Hyla armata* and *Bufo veraguensis*, with notes on the call of *Hyla armata* (Amphibia: Anura: Hylidae and Bufonidae). *Studies on Neotropical Fauna and Environment, 26:* 45–53.

CHANNING, A., 1978. A new bufonid genus (Amphibia: Anura) from Rhodesia. *Herpetologica, 34:* 394–397.

CHIN, P.-K. & INGER, R. F., 1989. A new species of gastromyzontine fish, *Gastromyzon danumensis*, from Sabah, Borneo. *Malayan Nature Journal, 43:* 53–58.

DUELLMAN, W. E. & LYNCH, J. D., 1969. Descriptions of *Atelopus* tadpoles and their relevance to atelopodid classification. *Herpetologica, 25:* 231–240.

GOSNER, K. L., 1960. A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica, 16:* 183–190.

INGER, R. F., 1954. Systematics and zoogeography of Philippine Amphibia. *Fieldiana: Zoology, 33:* 183–531.

INGER, R. F., 1960. Notes on toads of the genus *Pelophryne*. *Fieldiana: Zoology, 39:* 415–418.

INGER, R. F., 1985. Tadpoles of the forested regions of Borneo. *Fieldiana: Zoology, New Series, 26:* 1–89.

KURAMOTO, M., WANG, C.-S. & YU, H.-T., 1984. Breeding, larval morphology and experimental hybridization of Taiwanese brown frogs, *Rana longicrus* and *R. sauteri*. *Journal of Herpetology, 18:* 387–395.

MERTENS, R., 1960. Die Larven der Amphibien und ihre evolutive Bedeutung. *Zoologischer Anzeiger, 164:* 337–358.

NOBLE, G. K., 1929. The adaptive modifications of the arboreal tadpoles of *Hoplophryne* and the torrent tadpoles of *Staurois*. *Bulletin of the American Museum of Natural History, 58:* 291–334.

NOBLE, G. K., 1931. The biology of the Amphibia. New York: McGraw-Hill.

ORTON, G. L., 1953. The systematics of vertebrate larvae. *Systematic Zoology, 2:* 630–675.

ROBERTS, T. R., 1982. The Bornean gatromyzontine fish genera *Gastromyzon* and *Glaniopsis* (Cypriniformes, Homalopteridae), with descriptions of new species. *Proceedings of the California Academy of Sciences, 42:* 497–524.

VOGEL, S., 1981. *Life in Moving Fluids. The Physical Biology of Flow*. Boston: Willard Grant Press.

WASSERSUG, R. J., 1976. Internal oral features in *Hyla regilla* (Anura: Hylidae) larvae: An ontogenetic study. *Occasional Papers of the Museum of Natural History. University of Kansas, 49:* 1–24.

WASSERSUG, R. J. & DUELLMAN, W. E., 1984. Oral structures and their development in egg-brooding hylid frog embryos and larvae: evolutionary and ecological implications. *Journal of Morphology, 182:* 1–37.

APPENDIX

Specimens examined, grouped by species. FMNH = Field Museum of Natural History. USNM = United States National Museum of Natural History.

Ansonia leptopus: SARAWAK: Seventh Division, Kapit District, Nanga Putai (FMNH 77526), Nanga Tekalit (175 m) (FMNH 146281, 213701–13, 222441–62). SABAH: Lahad Datu District, Danum Valley Field Centre (170 m) (FMNH 231651).

Ansonia longidigita: SABAH: Ranau District, Mt. Kinabalu Park, Sungai Silau-Silau (1500 m) (FMNH 233511), Sungai Liwagu near Kundasan (1430 m) (FMNH 131248, 229877–78), Poring Station (400–615 m) (FMNH 130909–12, 229875–76, 229879–80); Sipitang District, Mendolong (670–1130 m) (FMNH 231706–60, 233512–19, 241566–89); Tuaran District, 6 km E of Tuaran (FMNH 140215).

Ansonia spinulifer: SABAH: Kota Marudu District, Marak Parak (230 m) (FMNH 241565); Lahad Datu District, Danum Valley Field Centre (170 m) (FMNH 231652–58, 235291–93, 241539–47); Sipitang District, Mendolong (690 m) (FMNH 235290). SARAWAK: First Division, Matang (FMNH 77521–22).

Ansonia 'beaks divided': SABAH: Ranau District, Mt. Kinabalu Park, Mesilau East (1460 m) (FMNH 231647). SARAWAK: Seventh Division, Kapit District, Nanga Tekalit (170 m) (FMNH 222480).

Ansonia 'cruciform': SABAH: Ranau District, Mt. Kinabalu Park, Poring Station (600 m) (FMNH 130907–08); Sipitang District, Mendolong (670–1030 m) (FMNH 235286–89); Tuaran District, 6 km E of Tuaran (FMNH 140214). SARAWAK: Fourth Division, Bintulu District, Sungai Pesu (FMNH 167993), Baram District, Long Siniai (FMNH 83019).

Ansonia 'sucker': SABAH: Tenom District, Crocker Range National Park, 10 km N of Tenom, Sungai Purulon (330–410 m) (FMNH 241557–64), Sungai Malutut (340 m) (FMNH 241555–56).

Aelurophryniscus chrysophorus: HONDURAS: Atlantida (USNM 290965).

Atelopus pachydermus: ECUADOR: Napo, Papallucta (USNM 286455).

Atelopus sp.: PERU: Cuzco, San Pedro (USNM field no. 19560).